

THE INFLUENCE OF DISTRIBUTION AND ECOLOGY
ON THE THERMOREGULATION OF SMALL BIRDS

By
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Abstract of Dissertation Presented to the Graduate Council
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THE INFLUENCE OF DISTRIBUTION AND ECOLOGY
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Data from the present study and the literature show that the energetics of thermoregulation in small birds are accurately described by the Newtonian model of heat loss. The level of body temperature is closely correlated with basal metabolic rate, thermal conductance, and body weight.

Tropical and desert birds generally have lower relative thermoregulatory quotients than expected (less than 1.0) on the basis of weight alone, and cold-climate species have high relative ratios. The relative ratio is a measure of the impact of ecology and climate on thermoregulatory capacity. Larger body weight can compensate for a low relative ratio, within limits.

Bird data now available indicate that ecology, particularly food habit, limits the distribution of birds outside the tropics and deserts, and that thermoregulatory

parameters are adapted primarily to climate.

Studies of the energetics of T_b regulation in non-desert tropical birds should give information as to the impact of ecology on this process, in that the climatic variable would be absent.

INTRODUCTION

Thermal homeostasis and its energetic cost for endothermic animals have been extensively documented over the last 20 years. The Newtonian model of heat loss has been used as a unifying method of looking at some of the parameters of body temperature regulation. This relationship is usually stated as:

$$dQ_L/dt = C (T_b - T_a)$$

in which $(dQ_L/dt)^1$ is the rate of heat loss, T_b is body temperature, T_a is the ambient temperature, and C is a proportionality factor known as thermal conductance. In thermoneutral or cooler ambient temperatures with no radiant energy source, it is obvious that $(dQ_L/dt) =$ rate of heat gain = metabolic rate (M), if the animal is going to hold T_b constant.

The zone of thermoneutrality for an endotherm is a range of T_a over which M is constant and independent of T_a . If the animal is postabsorptive and quiescent, M is equal to the basal metabolic rate (M_b) over this T_a range. In this zone, heat balance is maintained by physically changing the conductance (e.g., fluffing or compressing the fur or feathers). Ambient temperatures below the thermo-

¹ All symbols and expressions used in this paper are defined in Appendix A.

neutral zone result in an increase in M , and the proportionality of this increase to the $(T_b - T_a)$ difference is a measure of C . T_a above thermoneutrality also result in increased M values, mainly because of muscular activity associated with panting and the van't Hoff effect on chemical heat production.

The energetics of mammalian T_b regulation are better understood than those of birds. This stems from a number of reasons. Interest in avian thermoregulatory studies developed rather slowly, major stimuli being the series of papers by Scholander *et al.* (1950a, b, c) and studies of hummingbird metabolism by Pearson (1950). Avian species studied subsequently have not been as representative of the diversity in size, ecology, and distribution within the class as has been the case with mammals. In many instances, avian thermoregulatory studies have been incomplete because of the absence of precise measurements of the T_b that is being regulated. Failure to report precise T_b values for M measurements often will introduce bias into calculations, and greatly reduce the further usefulness of the data.

The review of energetics and thermoregulation in birds by King and Farner (1961) has been of considerable value in giving direction and perspective to this area of investigation. From the data then available, they derived an equation relating M_b and body weight (W) in small birds (*ca.* 100 grams or less) and another equation for birds larger than 100

grams. A standard equation relating conductance and W in birds is given by Lasiewski *et al.* (1967). Both of these equations will be discussed later.

A few attempts have been made at analyzing thermoregulation in terms of environmental demands, especially heat stress and evaporative cooling (e.g., Bartholomew *et al.*, 1962; Calder, 1964; Dawson and Fisher, 1969; Ligon, 1969).

Scholander *et al.* (1950c) have placed the emphasis on insulation for thermoregulatory adaptation to low T_a . It is now apparent (for example, Hart, 1957) that the basal metabolic rate may also be adaptive. The adaptive nature of body temperature is equivocal.

From Newton's heat loss relationship, one could anticipate that in response to environmental stress (thermal and/or nutritional) an animal could (1) behaviorally or physiologically alter the $(T_b - T_a)$ difference, (2) physically change its conductance, (3) chemically alter the rate of metabolism, or (4) achieve some suitable combination of these features. The behavior of these parameters in relation to ecology and climate has been investigated in some mammals, particularly by McNab (1966b, 1969, 1970; McNab and Morrison, 1963).

The relationships among thermal and ecological factors involved in thermoregulation have not been critically studied in birds. Ecological and distributional correlations have been made with differences in M_b and/or C in only a few species (Wallgren, 1954; Lasiewski and Dawson,

1964; Johnson, 1968; Ligon, 1968). No attempt has been made to synthesize into a rational whole the relationships that may be of general application in birds. McNab (1966a) has suggested that T_b in birds is determined by the ratio of $M_b : C$, much the same as in mammals. He has also indicated (1969) that in neotropical bats the $(M_b/C)_o$ ratio, and thus thermoregulatory capacity, is ecologically determined, especially by the reliability of the food supply.

The present study compares the behavior of thermoregulatory parameters in response to thermoneutral or cooler T_a for representatives of three avian families having different food habits. It was suspected, in view of the great mobility of temperate zone birds, that food habit might be more influential on distribution than on the thermoregulatory capacity. These studies on sparrows, warblers, and flycatchers were undertaken to explore this possibility. Representative data on thermoregulation from the literature have been incorporated in the analysis of physical and ecological correlates of general application in birds.

MATERIALS AND METHODS

All specimens used in this study were caught in mist nets. Most of the flycatchers were obtained in the coastal plain of North Carolina, the Harris' Sparrows¹ near Lawrence, Kansas, and the Black-throated Trogon along the Rio Negro near the junction with the Rio Branco in the state of Amazonas, Brazil. All other birds were caught in the vicinity of Gainesville, Florida, during 1968-69. The time of year in which measurements were made for each species is indicated in Appendix B.

The Harris' Sparrows were maintained in captivity, but all other specimens were caught during the day (usually afternoon) and were used for metabolic determinations the same night. Small birds were fasted for at least five hours and large birds six to seven hours before data collection was begun. Only data obtained between 2100 and 0500 hours were included in the study. Specimens were kept in complete darkness during the study interval. All data from birds suspected of being in *Zugunruhe* were excluded.

Metabolic rate was measured at three different ambient temperatures: 10°, 20°, and 30.5° C, or as otherwise indicated in a few cases. An open flow system was employed, and

¹ Scientific names of all birds used appear in Appendix B.

air flow rates were sufficient to maintain a concentration of at least 20 per cent oxygen in the metabolism chamber. This chamber had a volume of one gallon, and was immersed in a large, constant-temperature water bath. When a temperature change was desired, the chamber was switched to another water bath preset at the desired temperature. An interval of about two hours was allowed for the bird to adjust to the new temperature before data were used.

The partial pressure of oxygen in the air stream was measured by a Beckman G-2 Paramagnetic Oxygen Analyzer after carbon dioxide and water had been removed. Oxygen concentrations were recorded on a Honeywell strip chart recorder.

When a satisfactory metabolic reading was attained, the bird was quickly removed from the chamber and the pro-ventricular body temperature was measured by a YSI tele-thermometer. The bird could be removed and its T_b measured in less than one minute. Thus, each metabolic value has a corresponding T_b reading.

RESULTS

Data obtained in this study from 29 species of small birds are shown in Figures 1 - 14 and are summarized for each species in Table 1. These figures depict, species by species, the effects of different ambient temperatures on body temperature and metabolic rate (as measured by oxygen consumption). Metabolic measurements made within the zone of thermoneutrality are basal levels (M_b). At T_a below the lower limit of this zone, oxygen consumption increases. The slope of a line describing this M increase with declining T_a is considered to be the thermal conductance (C) of the species. General patterns of these responses are indicated later in this section.

For all species studied, the data indicate that 30.5°C is well within the zone of thermoneutrality. This is supported by the fact that most of the metabolic records obtained at this T_a were quite smooth, whereas records taken at 10° or 20° C usually showed oscillations between maximal and minimal values, presumably due to periodic bursts of shivering or other muscular activity. Thus, metabolic values taken at 30.5°C are probably basal rates, and represent the lowest constant level maintained for 15 minutes. For metabolic measurements below thermoneutrality, the repeatable minima are used. This procedure minimizes both M_b and C .

Fig. 1. Responses of body temperature and oxygen consumption to ambient temperature in *Spizella passerina* and *Zonotrichia albicollis*. The lower part of the graph shows the relationship between oxygen consumption (M) and ambient temperature (T_a). Horizontal lines indicate the mean basal metabolic rate for each species. The absolute value of the slope of each line in the lower part of the graph represents the mean thermal conductance for each species. The upper portion of the graph gives the body temperatures (T_b) corresponding to the M values below. The slanted line in the upper part is a reference which equates the temperature axes.

Fig. 2. Responses of body temperature and oxygen consumption to ambient temperature in *Passerculus sandwichensis* and *Ammodramus savannarum*. See the legend of Fig. 1 for explanation.

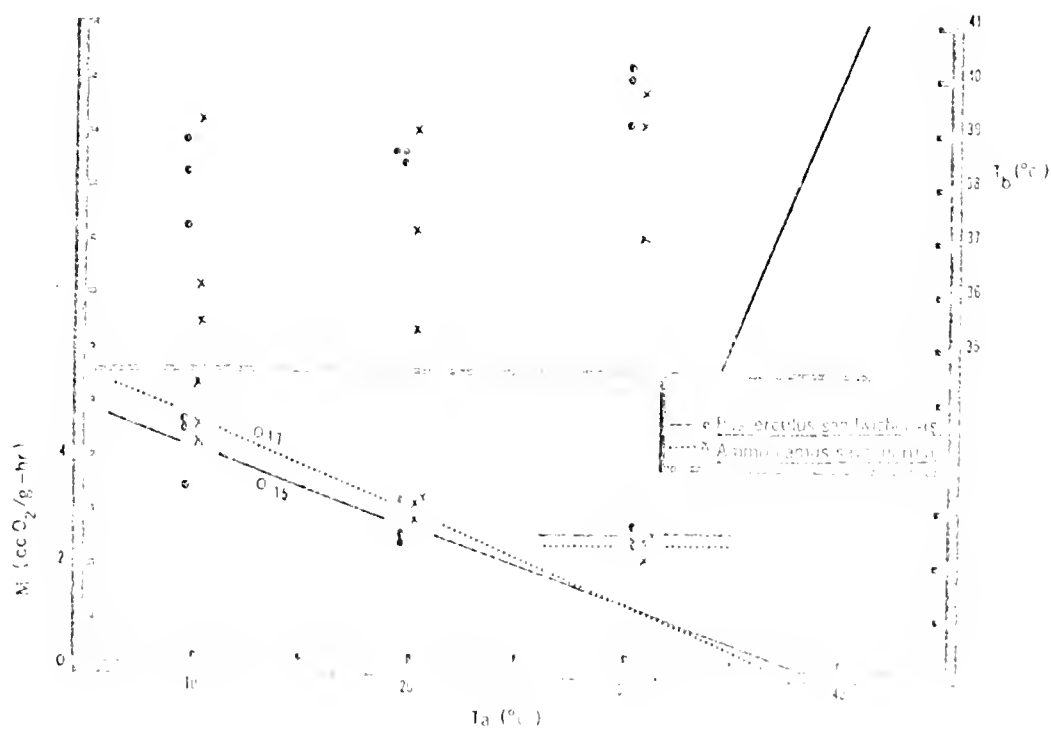
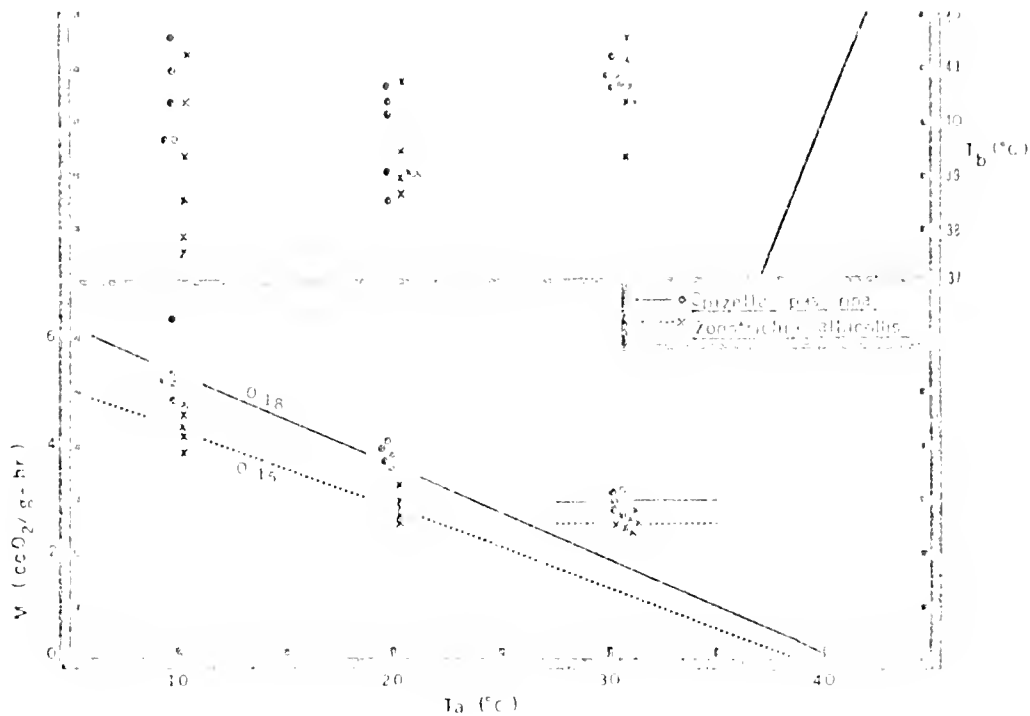


Fig. 3. Responses of body temperature and oxygen consumption to ambient temperature in *Melospiza melodia* and *Melospiza georgiana*. See the legend of Fig. 1 for explanation.

Fig. 4. Responses of body temperature and oxygen consumption to ambient temperature in *Pooecetes gramineus* and *Passerella iliaca*. See the legend of Fig. 1 for explanation.

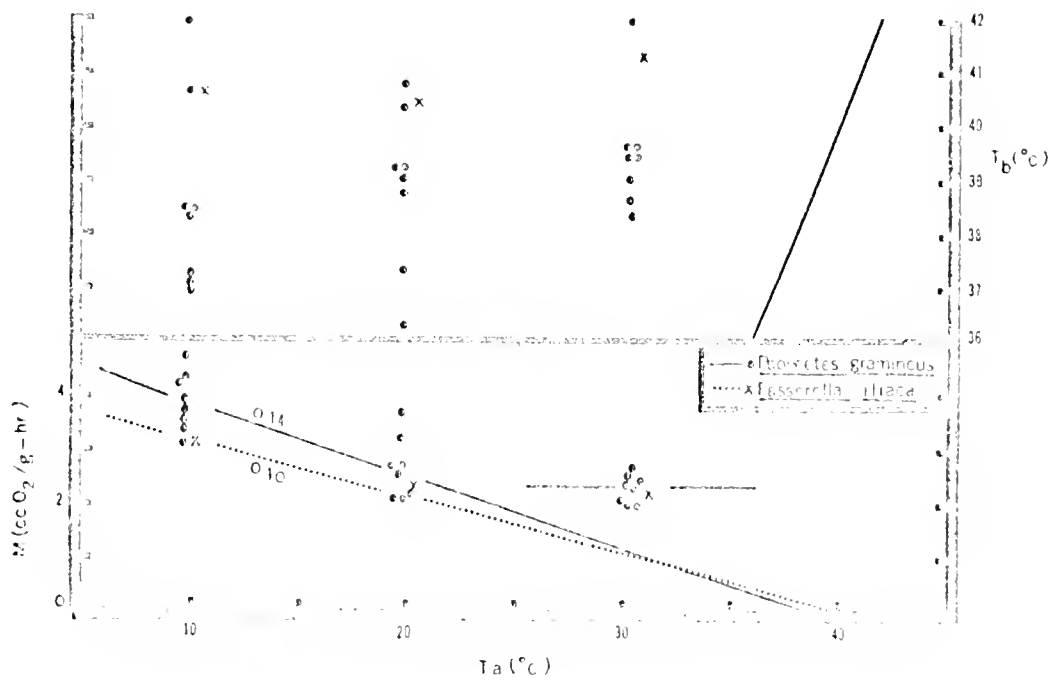
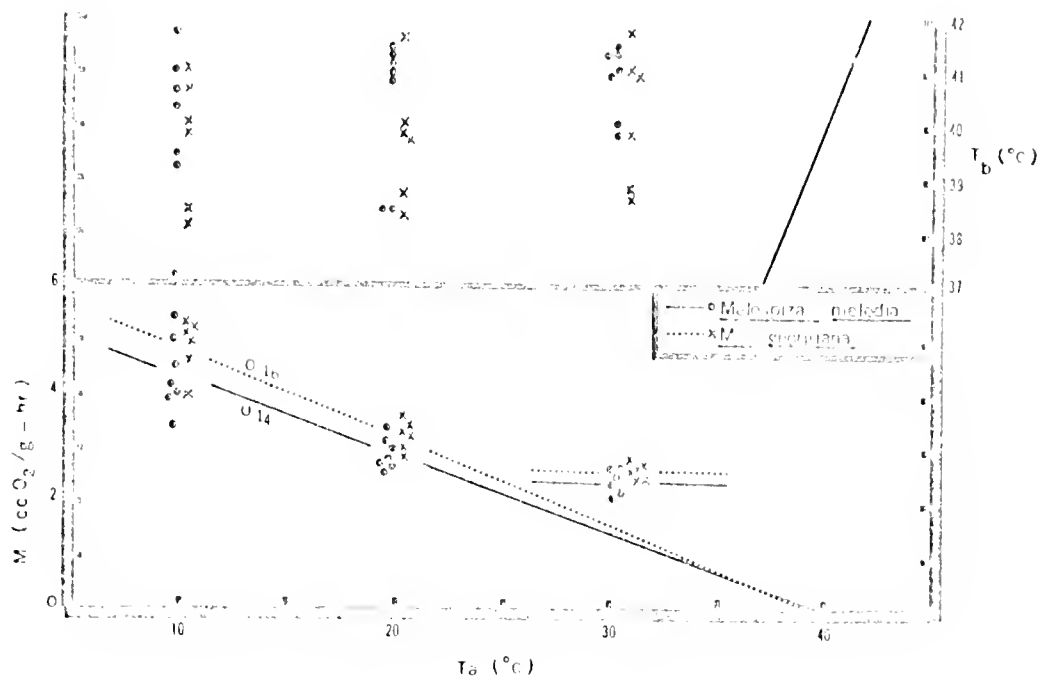


Fig. 5. Responses of body temperature and oxygen consumption to ambient temperature in *Zonotrichia querula* and *Zonotrichia leucophrys*. See the legend of Fig. 1 for explanation.

Fig. 6. Responses of body temperature and oxygen consumption to ambient temperature in *Parula americana* and *Vermivora pinus*. See the legend of Fig. 1 for explanation.

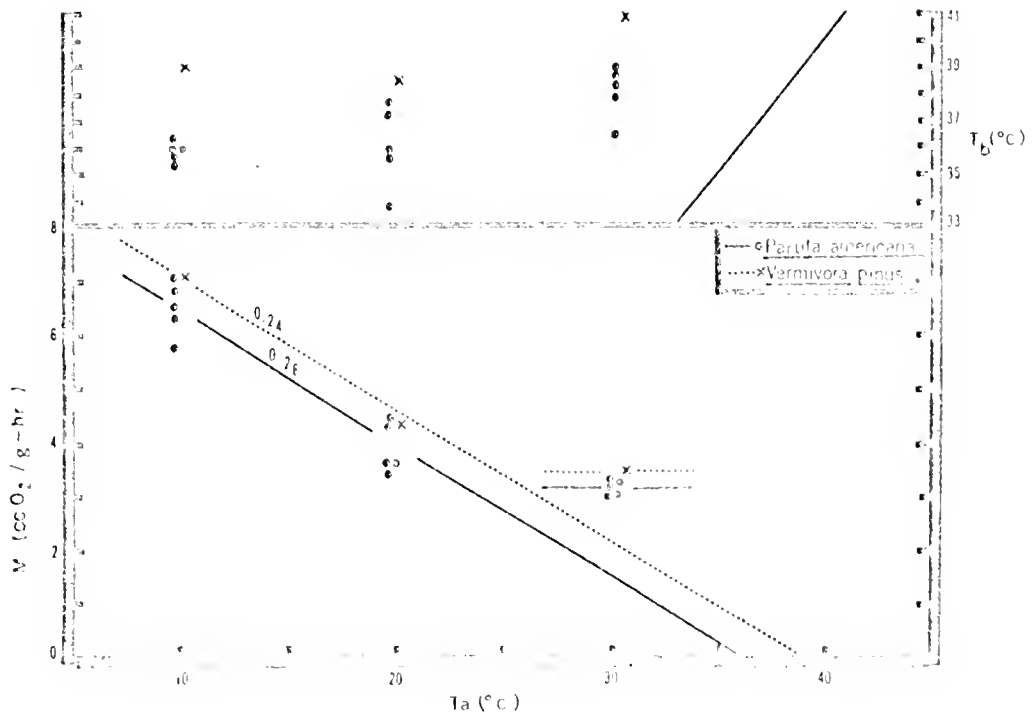
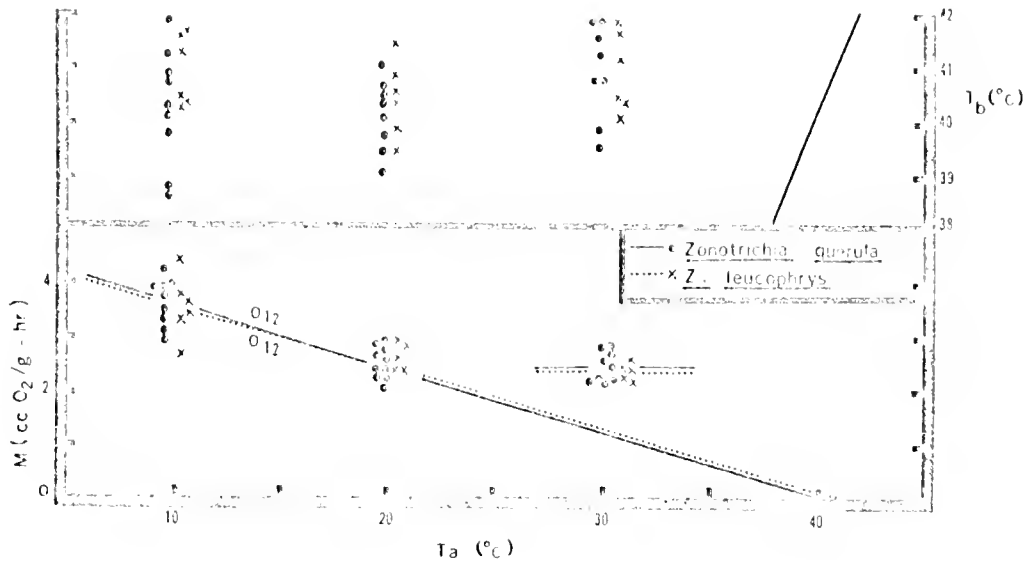


Fig. 7. Responses of body temperature and oxygen consumption to ambient temperature in *Dendroica pinus*, *Vermivora celata*, and *Mniotilta varia*. See the legend of Fig. 1 for explanation.

Fig. 8. Responses of body temperature and oxygen consumption to ambient temperature in *Dendroica coronata* and *Protonotaria citrea*. See the legend of Fig. 1 for explanation.

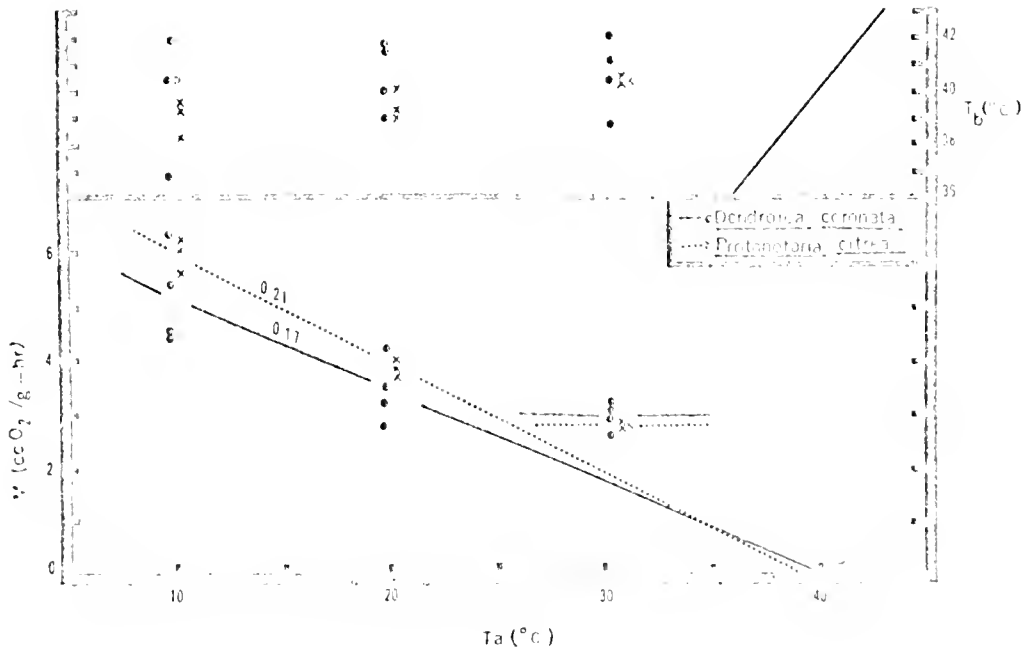
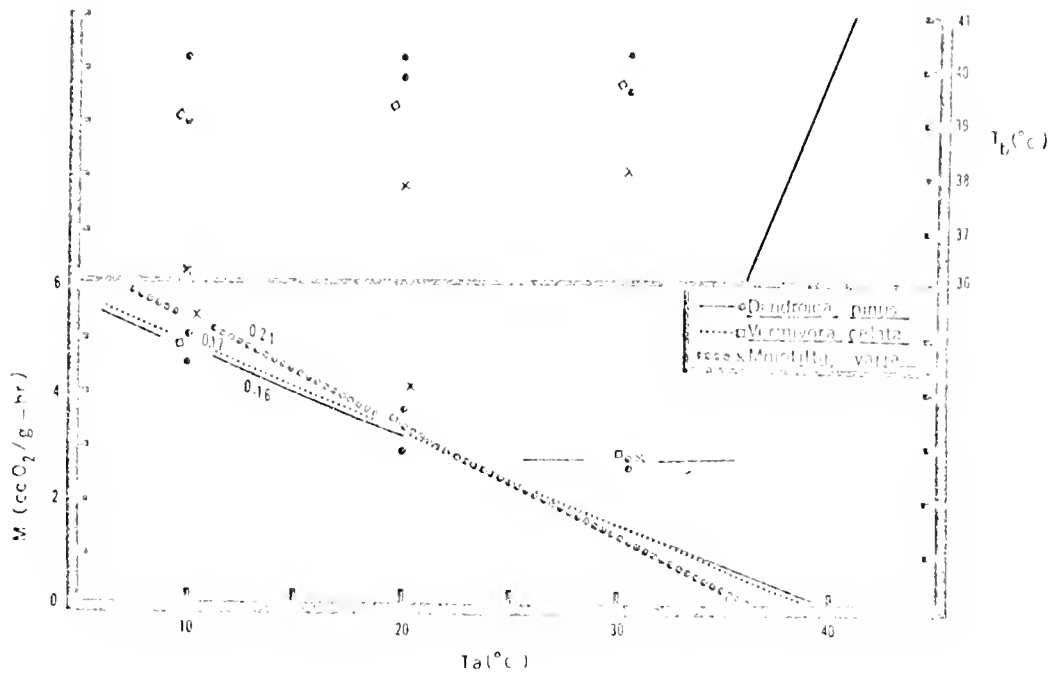


Fig. 9. Responses of body temperature and oxygen consumption to ambient temperature in *Wilsonia citrina* and *Dendroica dominica*. See the legend of Fig. 1 for explanation.

Fig. 10. Responses of body temperature and oxygen consumption to ambient temperature in *Seiurus noveboracensis* and *Seiurus aurocapillus*. See the legend of Fig. 1 for explanation.

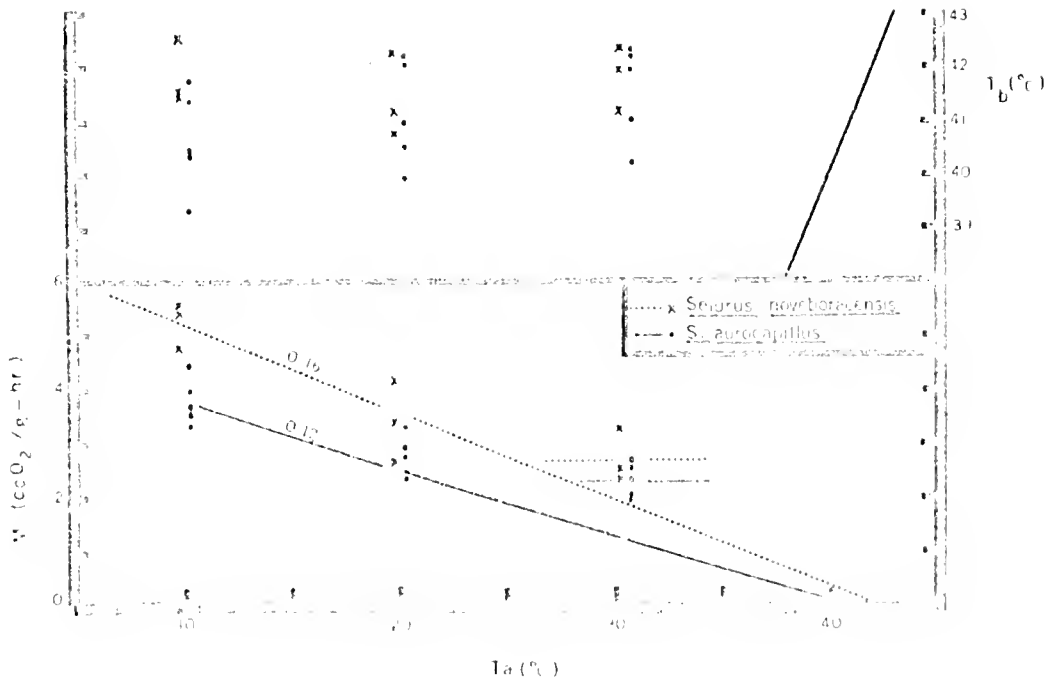
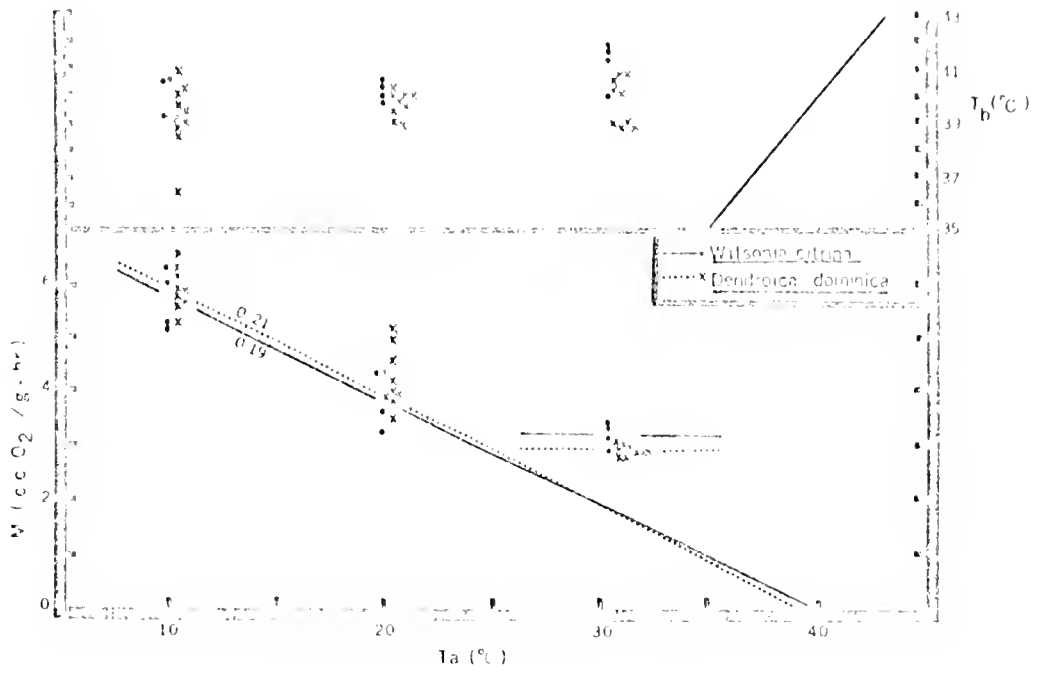


Fig. 11. Responses of body temperature and oxygen consumption to ambient temperature in *Dendroica palmarum* and *Trogon rufus*. See the legend of Fig. 1 for explanation.

Fig. 12. Responses of body temperature and oxygen consumption to ambient temperature in *Sayornis phoebe* and *Geothlypis trichas*. See the legend of Fig. 1 for explanation.

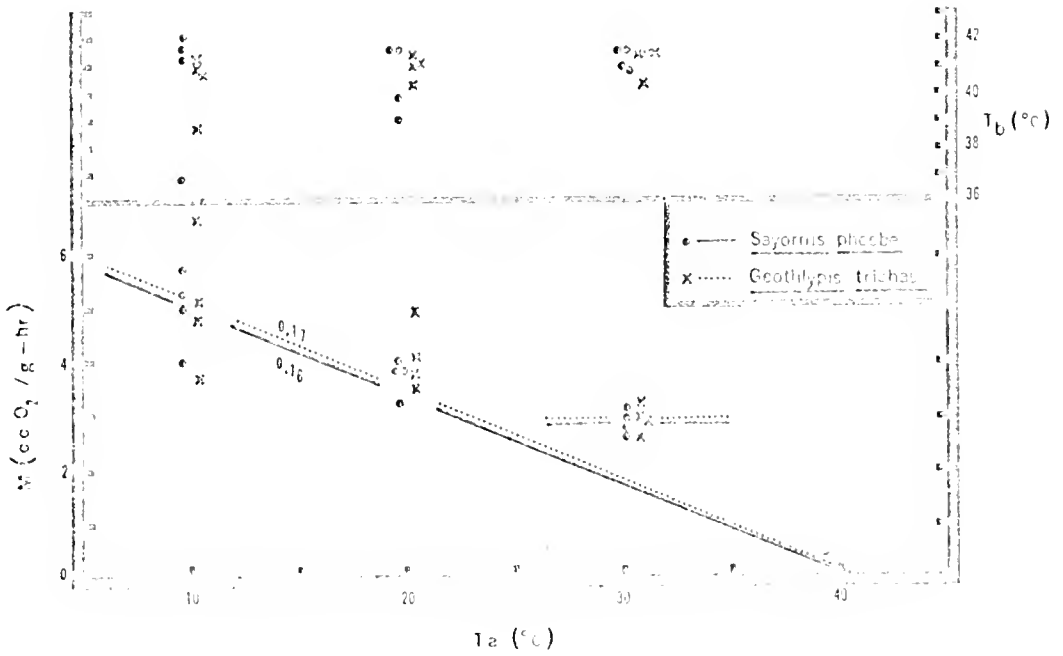
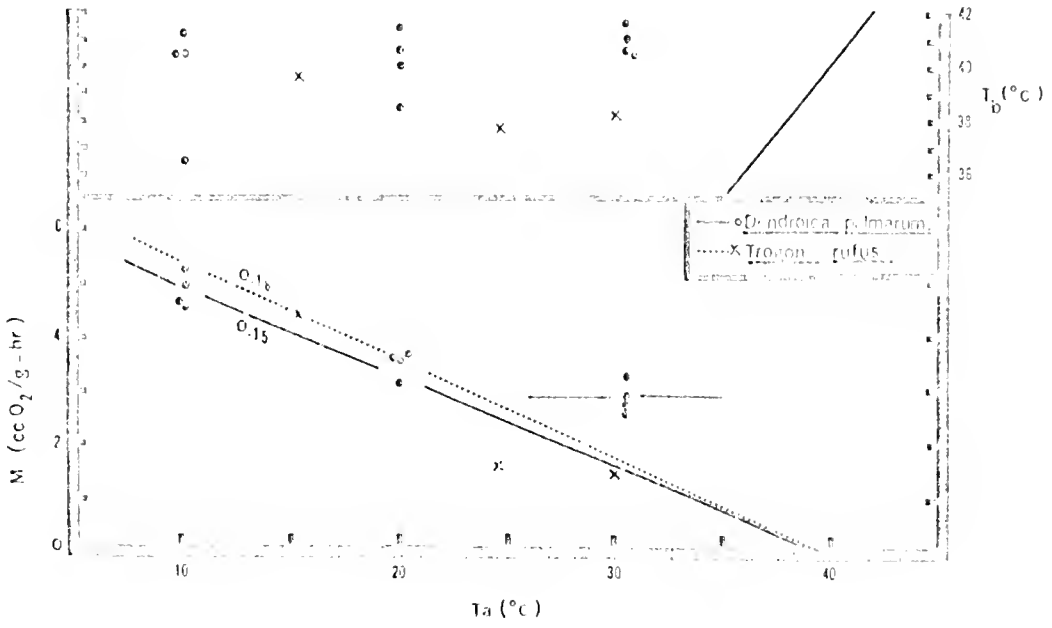


Fig. 13. Responses of body temperature and oxygen consumption to ambient temperature in *Empidonax virescens* and *Contopus virens*. See the legend of Fig. 1 for explanation.

Fig. 14. Responses of body temperature and oxygen consumption to ambient temperature in *Myiarchus crinitus* and *Tyrannus tyrannus*. See the legend of Fig. 1 for explanation.

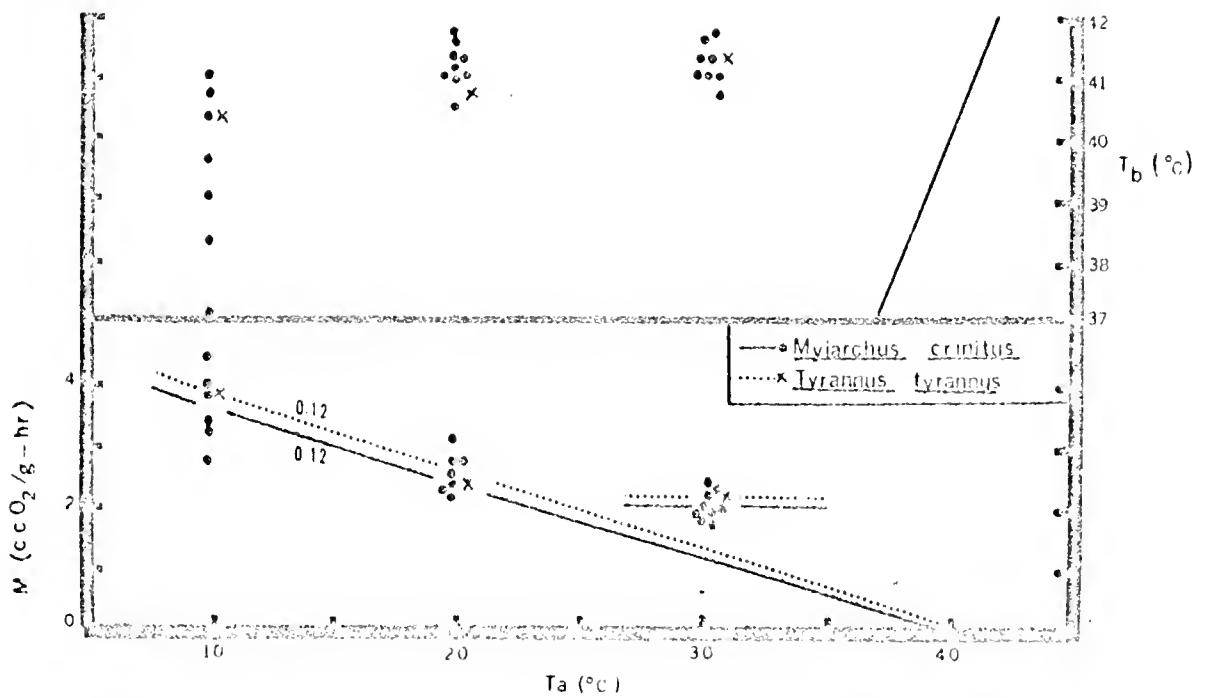
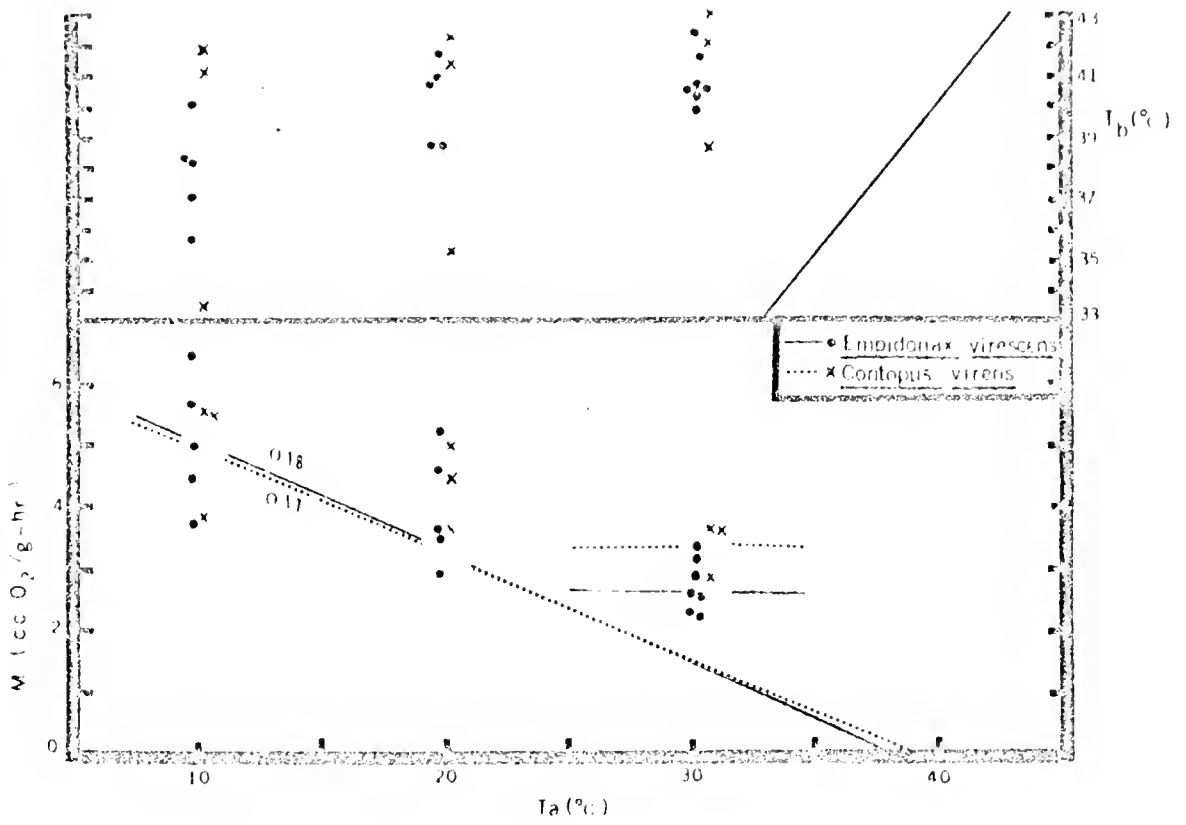


Table 1.-- Parameters of the energetics of T_b regulation in some small birds.

Species	N	W^*	M_b	M_b^{*8}	C	C^{*8}	$T_b - K$	$(M_b/C)_O^{*}$	$(M_b/C)_e^{*+}$	$(M_b/C)_r^{*}$	K^{\dagger}	T_b	$\Delta T_b / \Delta T_a$
Sparrows													
<i>Spizella passerina</i>	5	11.9 ^W	2.90	93	0.175	72	16.4	16.6	13.0	1.28	24.4	40.8	-0.018
<i>Ammodramus saviannarum</i>	3	13.8	2.31	78	0.174	78	13.3	13.4	13.4	1.00	25.3	38.6	-0.083
<i>Melospiza georgiana</i>	6	14.9	2.56	88	0.164	77	15.6	15.6	13.5	1.15	24.1	39.7	-0.006
<i>M. melodia</i>	7	19.1	2.38	89	0.144	76	16.4	16.6	14.1	1.18	24.5	40.9	-0.050
<i>Passerculus sandwichensis</i>	3	15.9	2.53	89	0.148	71	17.2	17.1	13.6	1.26	22.6	39.8	-0.083
<i>Poocetes gramineus</i>	8	.5	2.28	89	0.135	76	17.0	16.9	14.4	1.17	22.5	39.5	-0.045
<i>Zonotrichia albicollis</i>	6	20.2	2.50	96	0.144	79	16.9	17.4	14.2	1.23	23.6	40.5	-0.074
<i>Z. leucophrys</i>	6	26.1	2.34	97	0.119	71	20.3	19.7	14.8	1.33	20.6	40.9	0.0
<i>Z. querui</i>	9	33.3	2.42	110	0.119	83	20.6	21.3	15.4	1.38	20.7	41.3	-0.055
<i>Passerella iliaca</i>	1	30.7	2.18	97	0.098	67	22.3	22.2	15.3	1.45	19.0	41.3	-0.034
Warblers													
<i>Parula americana</i>	5	7.0	3.15	84	0.256	79	12.3	12.3	11.9	1.03	25.7	38.0	-0.110
<i>Vermivora pinus</i>	1	7.8	3.47	96	0.244	78	14.2	14.4	12.1	1.19	26.6	40.8	-0.093
<i>V. celata</i>	1	9.3	2.86	84	0.165	62	17.5	17.3	12.5	1.38	22.4	39.9	-0.015
<i>Mniotilta varia</i>	1	8.2	2.76	78	0.197	66	14.1	14.0	12.2	1.14	24.9	39.0	-0.073

Table 1.-- (continued)

Species	N	\bar{W}	M_b	$M_b^{\frac{2}{3}}$	C	C ^{3/2}	$T_b - K$	$(M_b/C)_o^+$	$(M_b/C)_e^{++}$	$(M_b/C)_r^{\dagger}$	K [§]	T_b	$\Delta T_b / \Delta T_a$
<i>Dendroica dominica</i>	9	9.8	2.94	86	0.202	75	14.5	14.5	12.6	1.15	25.2	39.7	-0.072
<i>D. palmarum</i>	4	9.8	2.95	85	0.164	61	17.6	17.4	12.6	1.38	23.3	40.9	-0.058
<i>D. coronata</i>	4	11.5	2.94	92	0.173	70	17.3	17.0	13.0	1.31	23.2	40.5	-0.079
<i>D. pinus</i>	2	12.0	2.70	87	0.162	67	16.9	16.6	13.0	1.28	23.4	40.3	-0.039
<i>Geothlypis trichas</i>	4	10.6	2.91	89	0.167	67	17.2	17.4	12.8	1.36	23.8	41.0	-0.034
<i>Wilsonia citrina</i>	4	12.0	3.21	103	0.191	82	16.3	16.8	13.0	1.29	24.9	41.2	-0.078
<i>Protonotaria citrea</i>	3	12.8	2.77	90	0.205	87	13.4	13.5	13.2	1.02	26.9	40.3	-0.064
<i>Seiurus noveboracensis</i>	3	18.7	2.67	100	0.162	84	16.2	16.5	14.0	1.18	25.5	41.7	+0.010
<i>S. aurocapillus</i>	5	19.0	2.27	85	0.122	64	18.6	18.6	14.0	1.32	22.9	41.5	-0.044
Flycatchers													
<i>Empidonax virescens</i>	7	12.3	2.58	83	0.179	75	14.2	14.4	13.1	1.10	26.3	40.5	-0.140
<i>Contopus virens</i>	3	13.9	3.32	113	0.171	76	19.3	19.4	13.3	1.46	22.2	41.5	-0.088
<i>Sayornis phoebe</i>	4	21.6	2.85	110	0.163	91	17.9	17.5	14.5	1.21	23.3	41.2	-0.038
<i>Myiarchus cineritus</i>	9	33.9	2.03	93	0.120	85	16.9	16.9	15.5	1.09	24.3	41.2	-0.078
<i>Tyrannus tyrannus</i>	1	35.7	2.18	101	0.125	91	17.6	17.5	15.6	1.12	23.7	41.3	-0.050

Table 1.-- (continued)

Species	N	W ^y	M _b	M _b ^{g*}	C	C ^{g**}	T _b -K	(M _b /C) _o [†]	(M _b /C) _e ⁺⁺	(M _b /C) _r [§]	K [§]	T _b	ΔT _b /ΔT _a
Trogon rufus													
	1	53.0	1.45	77	0.180	161	8.1	8.05	16.7	0.48	30.0	38.1	+0.005

† See Appendix A for explanation of symbols.
yy Numbers are mean values for each species.
* M_b^g = (mean observed N_b/7.29 W^{-0.341}) x 100.
** C^g = (mean observed C/0.848 W^{-0.508}) x 100.
+ (M_b/C)_o = observed M_b/observed C.
++ (M_b/C)_e = 7.29 W^{-0.341}/0.848 W^{-0.508}.
§ (M_b/C)_r = (M_b/C)_o/(M_b/C)_e.
§ Lower thermoneutral limit.

The mean M_b for ten species of sparrows is 92.6 per cent of that expected from the equation of King and Farner (1961) for small birds, and C is 75.0 per cent of the value expected from the equation of Lasiewski *et al.* (1967) (Figs. 1 - 5, 15, 16, and Table 1). Of the families studied here, the sparrows have the most northern wintering distribution, and contrast with the tropical Black-throated Trogon, which has a M_b only 77 per cent of that expected and a very high C (161 per cent) (Figs. 11, 15, 16, and Table 1).

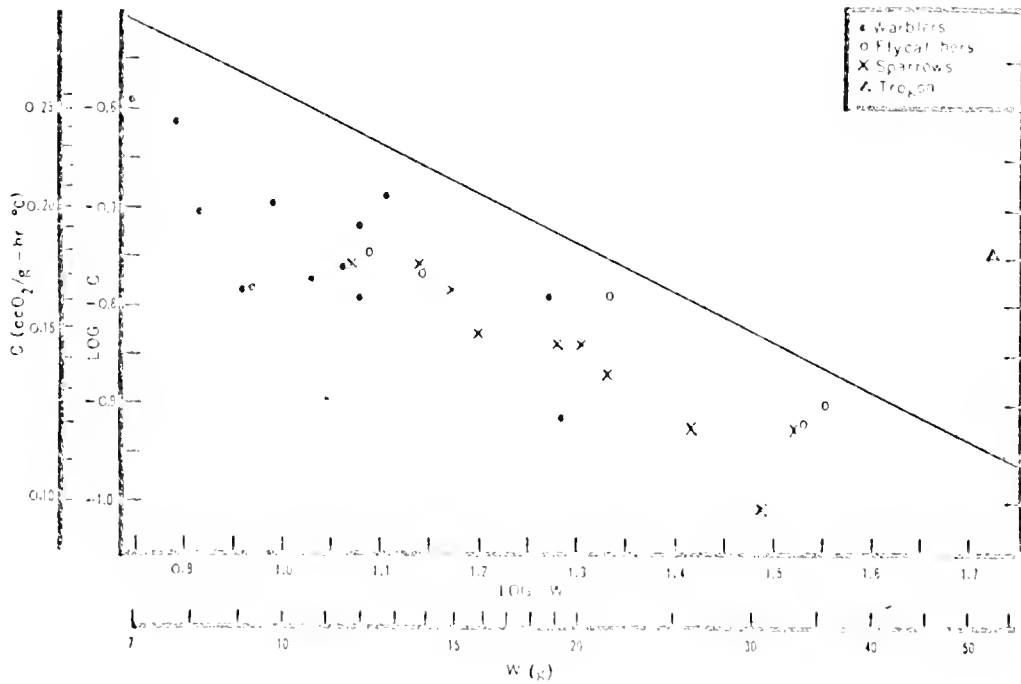
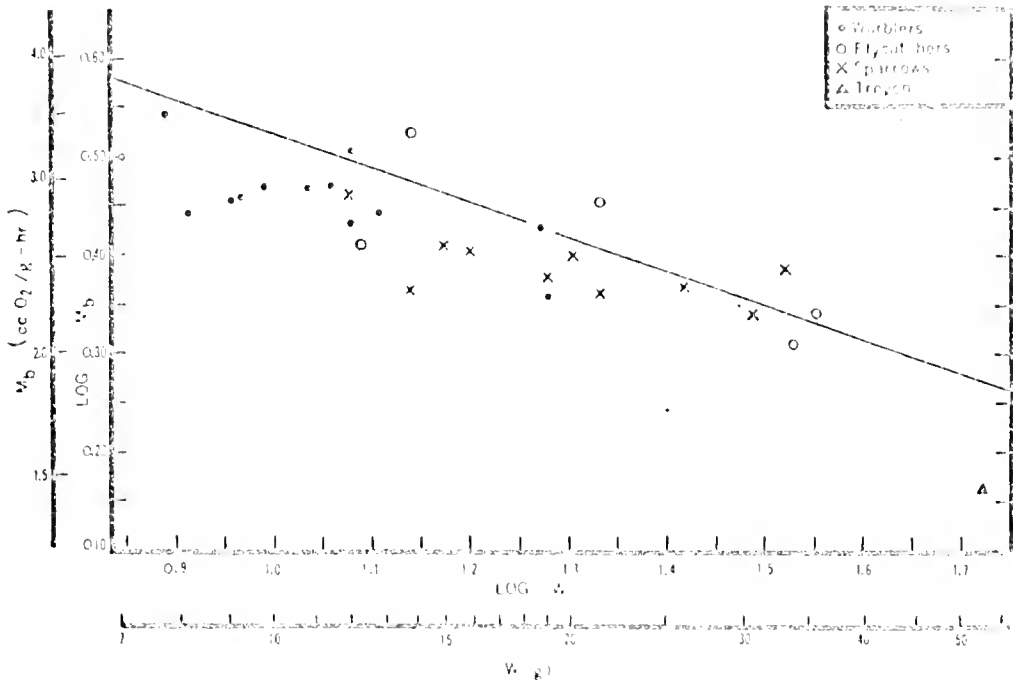
The mean M_b for all warblers is 89.2 per cent of that expected and C is only 72.4 per cent of the expected value (Figs. 6 - 12, 15, 16, and Table 1). Eight species wintering as far north as the southeastern United States have lower M_b and C values (85.8 and 66.5 per cent) than five species wintering farther south (94.6 and 82.0 per cent). These values indicate a considerable reduction in energy expenditure.

The five species of flycatchers have a collective M_b which is 100 per cent of that expected. C is 83.6 per cent of that expected, and the Acadian and Wood Pewee have a lower C (75.5 per cent) relative to that expected than the larger flycatchers (89.0 per cent) (Figs. 12 - 14, 15, 16, and Table 1).

Each metabolic datum is accompanied by a T_b value (Figs. 1 - 14). The mean T_b for sparrows and warblers in thermoneutrality was identical (40.3 °C), but was less than that of flycatchers (41.1 °C). Very small birds (<10 grams) usually have T_b that are lower and more sensitive to cool T_a than those of larger species.

Fig. 15. The relation of basal metabolic rate to body weight in some small birds. The line is a plot of the King-Farner (1961) equation for small birds ($\log M_b = \log 7.29 - 0.341 \log W$). Each point is the mean value for a species.

Fig. 16. The relation of thermal conductance to body weight in some small birds. The line is a plot of the equation of *Lasiewski et al.* (1967) ($\log C = \log 0.848 - 0.508 \log W$). Each point is the mean for a species.



DISCUSSION

Heat Loss and Heat Gain

Heat loss in animals is an extremely complex process. The factor C conceals a multiplicity of problems concerning heat loss by radiation, conduction, convection, and evaporation of water. The effective body surface area may be temporally varied, peripheral and appendicular blood circulation is subject to alteration, and the temperature of the body surface from which heat is lost may be different than that measured in the core. Some of these problems have been discussed in detail by Burton (1934), Scholander *et al.* (1950a, b, c), Kleiber (1961), Bartholomew and Tucker (1964), and McNab (1970).

It would be desirable to have a rigorous experimental capability such that the physical parameters could be measured which are necessary for using models such as Fourier's law of heat flow. The ability to apportion properly the responsibility for heat loss among radiation, convection, and conduction as well as evaporation is also a worthy aspiration. However, as indicated in the previous paragraph, there are a number of reasons why this is impractical, if not impossible, at present. It is important that we begin to measure quantitatively the partitioning of heat loss by birds. This partitioning is probably highly adaptive.

Knowledge of trends of performance by each avenue of heat loss would allow us to understand the thermal and ecological interrelationships of individual species. The recent studies by Hamilton and Heppner (1967) and Heppner (1970) on radiative energy exchange and its effect on the heat budgets of dark and light birds are steps in this direction.

However, the details of the partitioning of heat loss are overlaid by more general thermo-ecologic patterns. In the final analysis, it is the total rate of heat loss that must be balanced by heat production. It is exactly at this point that the Newtonian model is useful. Its employment simply ignores the various reasons for heat loss, and considers the totality of heat lost as a single parameter.

This approach, although simplistic, allows examination of the relationship of metabolic heat gain (M), and total heat loss $C (T_b - T_a)$, to biological and distributional characteristics of a species, such as ecology and climate. It will be seen that the available data fit this simple approximation remarkably well. As long as the physical limitations of this concept are understood, I believe that it can be of considerable heuristic value in a biological sense.

The Newtonian model was originally used to describe the cooling of a body. Since a decline in temperature does not generally occur in homoiotherms, it is sometimes argued that this law is not applicable to such systems. The argument becomes rhetorical when the cooling expression is rewritten as a heat loss statement using the specific heat (c) and body weight (W):

$$dT_b/dt = k (T_b - T_a) \quad (1)$$

$$dT_b/dt = dQ/dt \cdot 1/cW \quad (2)$$

$$\therefore dQ/dt \cdot 1/cW = k (T_b - T_a) \text{ and} \quad (3)$$

$$dQ/dt = kcW (T_b - T_a) \text{ or} \quad (4)$$

$$dQ/dt = C (T_b - T_a) \quad (5)$$

where C is a composite proportionality factor commonly known as thermal conductance.

Metabolism

Of the species of birds used in this study, only a few sparrows have been subjected to metabolic examination by other investigators. Table 1 shows that sparrows larger than 20 grams have M_b almost exactly as predicted from W by the King-Farner equation, except for the Vesper, which also has a lower T_b . King's (1964) data on the White-crowned Sparrow agree with those obtained in this study. Rising's (1968) values for Harris' Sparrow are much higher than expected (158 per cent) and were obtained by weighing CO_2 produced. My data for the White-throated Sparrow are similar to those of Hudson and Kimzey (1964). The values given by Lasiewski and Dawson (1967) for White-throated, Song, and Fox Sparrows are considerably higher than those from this study. This may be due in part to differences in procedures of taking data from the strip charts. Figure 15 shows the position of my data in relation to the King-Farner curve for small birds.

It will be noted from Table 1 that those sparrows with M_b lower than expected usually also have lower T_b than the other species. M_b for most of the warblers are also

somewhat lower than expected, particularly in species wintering in Florida or in very small species. This reduces energy expenditure considerably and may be very important for small insectivorous species wintering in cool climates. The reduction in M_b is made possible in such species by a comparatively better insulation. The two species of insectivores that winter in the southeastern U. S. and still maintain relatively high M_b (Phoebe and Myrtle Warbler) are known to depend heavily on berries for food during winter (Bent, 1942, 1953; Yarbrough and Johnston, 1965).

The tropical and desert species in Table 2 have significantly reduced M_b values in most cases. This may function mainly for reducing energetic demands (small hummingbirds) or for moderating the heat load and evaporative water loss (desert owls and goatsuckers). The species which appear to take exception to such strategies are either very small (Black-rumped Waxbill) or have exceptionally high C values, even in view of their small body size (Paradise Widowbird and Zebra Finch).

Lasiewski and Dawson (1967) have statistically separated standard metabolism curves of passerine and non-passerine birds. No biological rationale is evident for this decision. Indeed, there may be differences in M_b between passerines and non-passerines; there probably are different curves for penguins and hummingbirds, auks and vultures, etc. Non-passerines have been inadequately sampled over the size range from which most of the passerine data have been

Table 2.-- Energetic parameters of small birds selected from the literature.

Species	W^y	N_b	M_b^*	C	$C\bar{x}^{**}$	$(M_b/C)^+$	$(M_b/C)^{++}$	$(M_b/C)^{\dagger}$	K^{\ddagger}	T_b	References
<i>Eurostocheus guttatus</i>	88.0 ^{yy}	0.83	53	0.143	168	5.8	18.3	0.32	33	38.9	Dawson and Fisher, 1969
<i>Phalaenoptilus nuttallii</i>	40:	0.8	39	0.122	94	6.5	16.4	0.40	35.4	35-42	Bartholomew et al., 1962
<i>Chordeiles minor</i>	72:	1.1	65	0.11	114	10.0	17.5	0.57	28	38	Lasiewski and Dawson, 1964
<i>Nyctidromus albigularis</i>	43	1.44	71	0.106	84	13.6	16.1	0.85	23	37	Scholander et al., 1950
<i>Otus trichopsis</i>	99.8	0.66	43	0.056	68	11.7	18.5	0.62	26.6	37.9	Ligon, 1969
<i>Microthene whitneyi</i>	46	0.94	48	0.097	72	10.8	16.8	0.65	27.2	37.8	Ligon, 1968, 1969
<i>Clauelidium gnoma</i>	52.0	1.60	85	0.126	112	12.7	17.2	0.74	26	38.3	Ligon, 1969
<i>Agelaius aradicus</i>	118.1	0.96	67	0.051	68	18.8	19.1	0.99	20	38.2	Ligon, 1969
<i>Taeniopygia castaneotis</i>	11.7	3.28	104	0.34	142	9.65	13.0	0.74	30.5	40.2	Calder, 1964
<i>Estrilda troglodytes</i>	6.1	3.5	90	0.40	85	8.8	11.7	0.75	28	37	Lasiewski et al., 1964
<i>Vidua paradisica</i>	10.5	3.34	104	0.30	115	11.1	12.7	0.87	31:	42:	Scholander et al., 1950
<i>Eugenes fulgens</i>	6.6	2.7	70	0.30	90	9	11.8	0.76	30.5	39	Lasiewski and Lasiewski, 1967
<i>Laniopsis elemonensis</i>	7.9	2.3	65	0.23	76	10	12.2	0.82	31	41	Lasiewski and Lasiewski, 1967
<i>Patagona gigas</i>	19.1	2.7	103	0.17	90	15.9	14.1	1.13	27+	42.5	Lasiewski et al., 1967
<i>Hesperiphona vespertina</i>	55.1	2.45	132	0.11	103	22.3	17.4	1.28	15.5	38.6	West and Hart, 1966
<i>Cyanocitta cristata</i>	80.8	1.89	116	0.068	75	27.8	17.9	1.55	12.2	40.3	Misch, 1960

Table 2.-- (continued)

Species	\bar{w}^y	M_b	M_b^*	C	$C\bar{x}^{**}$	$(M_b/C)_o^{\dagger}$	$(M_b/C)_e^{\dagger\dagger}$	$(M_b/C)_r^{\ddagger}$	K^{\S}	T_b	References
<i>Loxia leucoptera</i>	29.8	2.8	122	0.11	73	25.4	15.2	1.67	14	40	Dawson and Tordoff, 1964
<i>L. curvirostra</i>	29.4	3.1	135	0.12	79	25.8	15.1	1.71	15	40	Dawson and Tordoff, 1964
<i>Perisoreus canadensis</i>	71.2	2.1	124	0.06	64	34.9	17.7	1.95	7	41.6	Veghte, 1964

^y See Appendix A for explanation of symbols.

^{yy} Numbers are mean values for each species.

^{*} M_b^* = (mean observed $M_b/7.29 \bar{w}^{-0.341}$) $\times 100$.

^{**} $C\bar{x}$ = (mean observed $C/0.848 \bar{w}^{-0.508}$) $\times 100$.

[†] $(M_b/C)_o$ = observed M_b /observed C.

^{††} $(M_b/C)_e$ = $7.29 \bar{w}^{-0.341}/0.848 \bar{w}^{-0.508}$.

[‡] $(M_b/C)_r$ = $(M_b/C)_o/(M_b/C)_e$.

[§] Lower thermoneutral limit.

obtained. Perhaps even more important than body size are the climatic and ecological factors impinging on the birds in question. It might be expected that birds from the tropics or arid areas with great heat loads, soaring or gliding species, flightless birds, would have reduced metabolic heat production when compared to active foragers contending with cool, cold or variable T_a in the absence of a capacity for torpor. Many more data are needed for passerine and non-passerine birds having similar distributional histories, ecological characteristics, thermal environments, and body sizes before it can be said that physiological responses are determined by taxonomy at the ordinal level.

Conductance

As has been seen above, it is sometimes meaningless or even misleading to view heat gain without evaluating heat loss. I have already indicated that the procedure of data-taking used here minimizes C. Data are available in the literature for only two of the species studied by me. King's (1964) C data on the White-crowned Sparrow are similar to those reported here, but Rising's (1968) C values for Harris' Sparrow are nearly double those in the current study.

The mean C for every species in the present study is lower than that predicted by the equation of Lasiewski *et al.* (1967), except for the Black-throated Trogon (Fig. 16). This completely tropical species has a C on a par with the Spotted Nightjar of Australian arid lands (Dawson and Fisher, 1969).

It seems to be generally true that birds from the tropics or hot deserts have relatively high C values, and species that encounter cool weather have low C. However, there are some prominent exceptions to this generalization. Very small desert or tropical species, such as hummingbirds may not be able to tolerate increases in C (also compare the Black-rumped Waxbill with the larger Paradise Widowbird and Zebra Finch). The smaller caprimulgids with more temperate wintering distributions (Poor-will and Pauraque) have relatively better insulation than the larger Nighthawk and Spotted Nightjar that winter at lower latitudes.

The small nocturnal owls have good insulation (Table 2). Of course, the Saw-whet is found in cold climates, and the Whiskered and Elf Owls are active during the cool desert nights. The only small owl in Table 2 with a relatively poor insulation is the Pygmy, which is largely diurnal in its activity and thus is exposed to the high T_a of the southwestern U. S. and Mexico.

The importance of providing T_b measurements along with M values is seen in the calculation of C. Some species of birds probably do not change abruptly from physical to chemical thermoregulation (Figs. 7, 9, 12, 13). Many species also experience a reduction in T_b when T_a is below the thermoneutral range. These effects are additive, and under such circumstances the slope of the regression line through the data points does not represent C. Minimal C is the slope of

a line connecting the mean M value at a given T_a below thermoneutrality with the corresponding mean T_b at $M = 0$. The lower limit of thermoneutrality for purposes of calculation can be determined by translating this line to the right on the x-axis to the point which is the T_b measured at thermoneutral T_a .

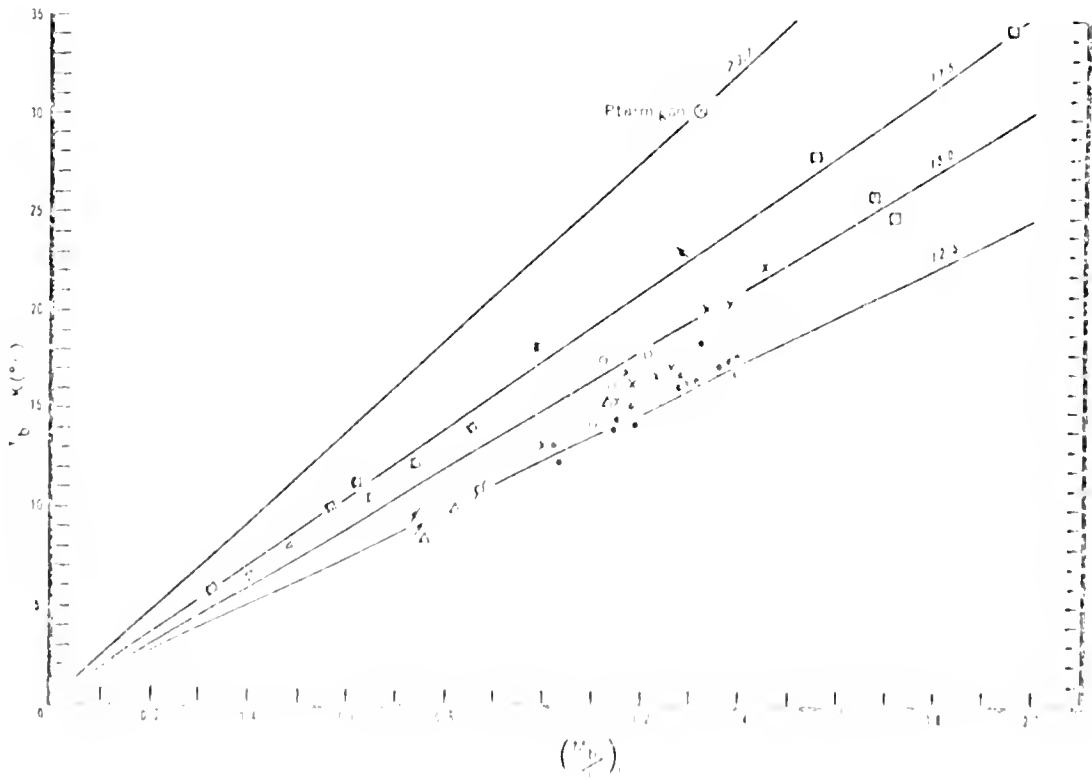
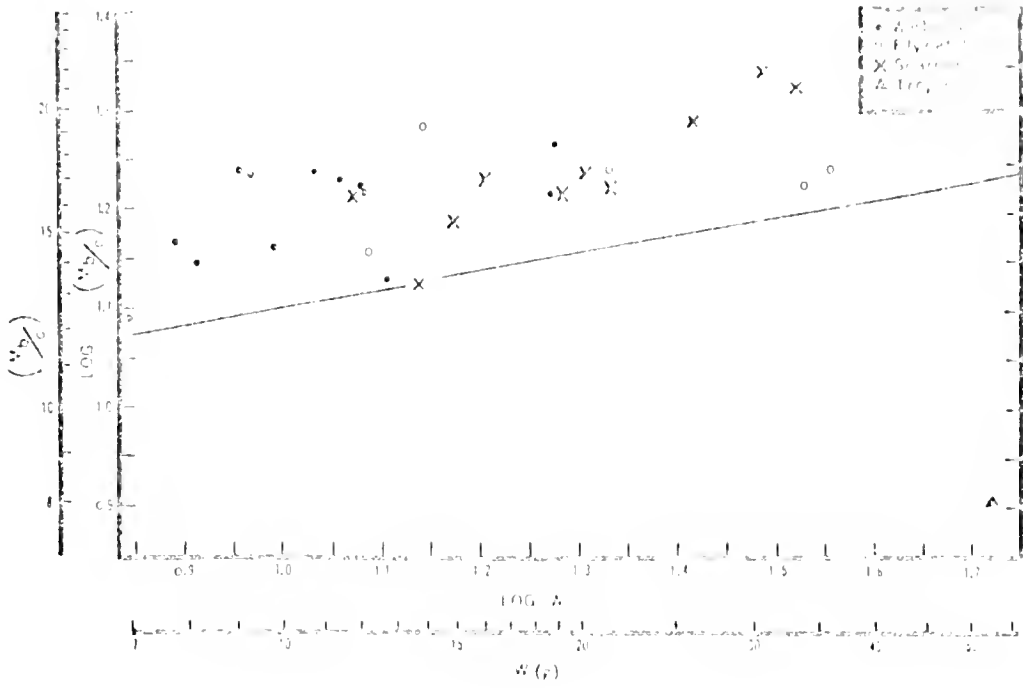
The Physical Model

The relation of M_b to C for birds in the current study is compared to a line representing predicted values (Fig. 17). It has been stated previously that this relationship of heat gain (M) to the coefficient of heat loss (C) is a better expression of the thermoregulatory capacity of an animal than either parameter alone. Each of these factors can probably be modified by selection and/or acclimatization, but only with proper reference to the capacity of its companion factor and body size. For example, the response to an environmental alteration of C can be made only to the extent that body size is not limiting and that the animal can obtain an adequate food or water supply to operate at the new M level. All this must be done within the framework that exists for maintenance and reproductive success.

Therefore, the observed thermoregulatory quotient $(M_b/C)_o$ is broadly composed of two components: $(M_b/C)_e$, the quotient expected of a "typical" bird of the specified W , and $(M_b/C)_r$, an index of that variation from "typical" that may be attributed to the adaptive impact of ecological and climatic demands. The modified heat loss equation can

Fig. 17. The relation of the observed thermoregulatory quotient $(M_b/C)_o$ to body weight in some small birds. The line is a plot of the quotient expected on the basis of weight from the equations of King and Farner (1961) and Lasiewski *et al.* (1967), $\log (M_b/C)_e = \log 8.59 + 0.167 \log W$.

Fig. 18. A plot showing the effect of body weight on thermoregulation data taken from birds used in this study and from the literature. Lines have slopes equal to $(M_b/C)_e$. Data for the White-tailed Ptarmigan (*Lagopus leucurus*) are from Johnson (1968). Symbols are as in Fig. 20. See Tables 1 and 2 for data and references.



be rearranged and partitioned so that:

$$T_b = (M_b/C)_o + K \text{ and} \quad (6)$$

$$T_b = (M_b/C)_r (M_b/C)_e + K \quad (7)$$

where K is the lower limit of thermoneutrality (McNab, 1969, 1970).

Since equation (7) has the general form $y = ax + b$, the fit of available data to this model can be checked. A biological check is also possible by rearranging equation (7) so that:

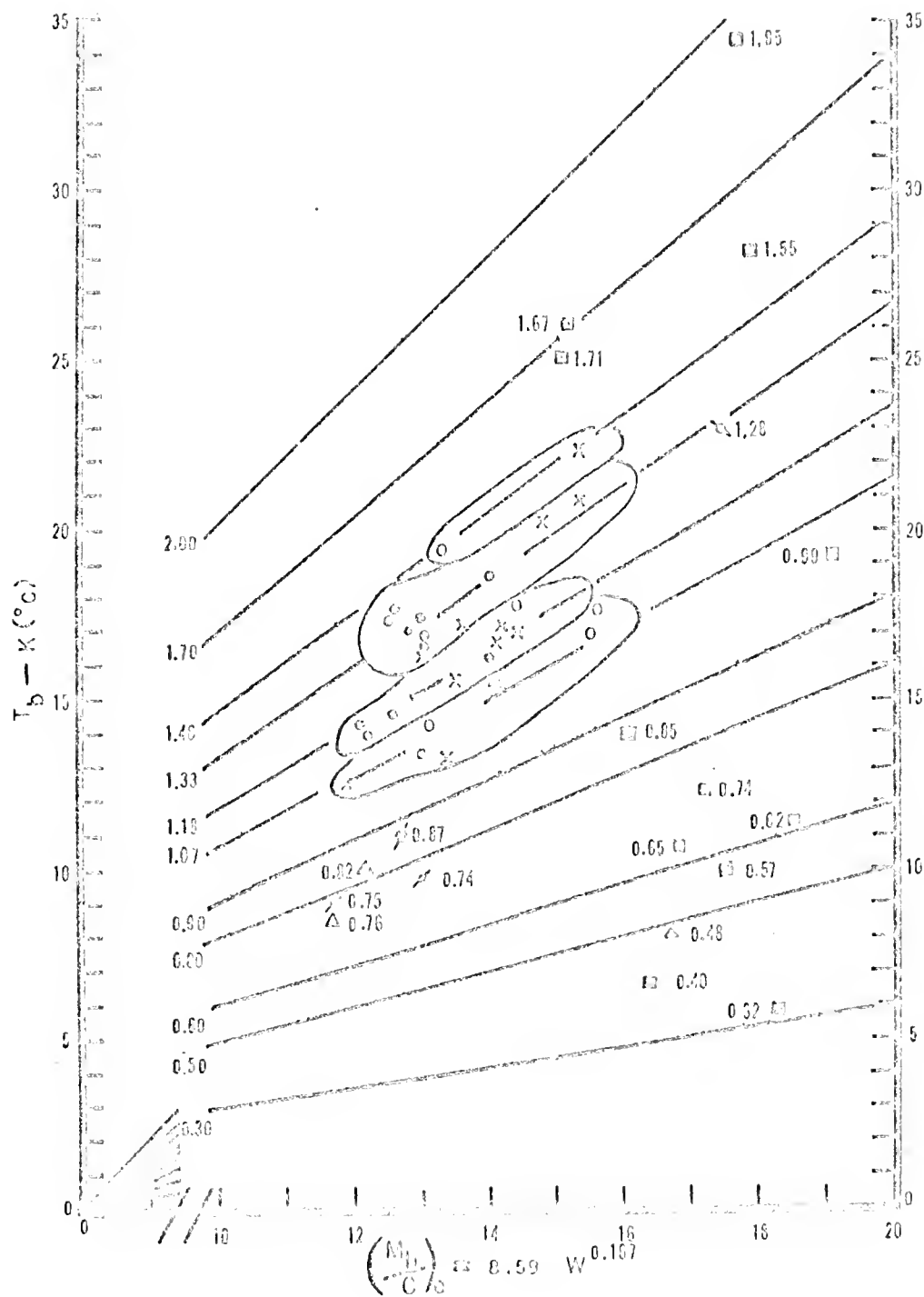
$$T_b - K = (M_b/C)_r (M_b/C)_e \quad (8)$$

where T_b measurements on the left side of the equation are compared with metabolic measurements on the right. Graphically represented, when $(T_b - K)$ is plotted against $(M_b/C)_e$, a line from the origin having a slope of $(M_b/C)_r$ should intercept the corresponding data point (Fig. 19). In a more dramatic way, when $(T_b - K)$ is plotted against $(M_b/C)_r$ $(M_b/C)_e$ (equation 8), the data should fall along a straight line having a slope of 1.0. In Figure 20, which is a plot of this relationship, the closeness of fit is evident.

Determination of the Level of T_b

It is apparent that K is determined by M_b and C, both by the weight factor $(M_b/C)_e$ and the relative ratio $(M_b/C)_r$. Therefore, adaptation to climatic and ecological conditions, along with W, sets the lower limit of the energetic quantity $(T_b - K)$. This difference is the buffer between the bird's regulated T_b and the necessity for increasing energy expenditure. The magnitude of $(T_b - K)$ is a good indicator of the

Fig. 19. The relation of the extent of the thermal buffer to the thermoregulatory quotient expected from body size alone. Numbers at the left terminus of each line are slopes. The number accompanying each point is the $(M_b/C)_r$ value. The mean $(M_b/C)_r$ value for encircled points is equal to the slope of the line through the circle. Symbols are as in Fig. 20. See Tables 1 and 2 for data and references.



extent of cold stress to which a bird is subjected in its habitat.

The question as to whether T_b is a dependent or independent parameter is more complex. It is logical to agree with Hammel's (1968) contention that an initial step in the evolution of homoiothermy was necessarily the acquisition of an adequate insulation. Then, it becomes energetically feasible to invest in a fairly high M_b . The eventual thermoregulatory quotient and size of the endothermic avian stock likely resulted in a $(T_b - K)$ that was satisfactory for the thermal environment in which these animals lived. This original T_b would have been dependent on M_b , C , and W . As the advantages of thermal homeostasis asserted themselves (whatever they may be), it is reasonable to assume that temperature-specific neural, enzymatic, and other systems also evolved. These systems could be more efficient if T_b were precisely regulated. So, there must have been a parallel evolution of the energetic machinery making endothermy possible and a regulating system that would maintain T_b stability in the interest of physiological efficiency.

Ontogenetic evidence lends support to this speculation. Nestlings of some altricial species of birds show a chronological improvement in insulation, and at some rather well-defined stage begin a rapid development of metabolic heat production and thermoregulatory capacity (e.g., Dawson and Evans, 1957, 1960; Yarbrough, 1970b). In cool environments, such nestlings first are able to regulate their T_b at a lower level (e.g., 31 - 33 °C) than that of the adult

(about 40 °C). The regulated T_b increases with age until the adult level is achieved. So, it would seem that the regulatory mechanism becomes functional at a stage when $(M_b/C)_0$ and W reach an acceptable level, but the set point of the thermostat (the reference temperature for the regulating mechanism) is elevated as $(M_b/C)_0$ and W increase.

For the original data presented here, as well as for the data from the literature, equation (6) predicts T_b with an average error of only 0.3 °C. One might well have expected experimental and mechanical error to exceed this value. Thus, the level of T_b is very closely correlated with the interaction of M_b , C , and W in birds, as it is in mammals (McNab, 1966b, 1969). However, I feel that the existing evidence does not warrant classification of T_b as a completely dependent factor, except possibly in an evolutionary sense. Of course, it is true that in thermoneutrality a given T_b depends on a particular balance of C and M_b , but the T_b set point may influence the level of M_b . The distinction lies between physical and physiological dependence. In the absence of the proper interrelations among M_b , C , and W , the thermostat is ineffectual. Under usual circumstances the regulating mechanism acts as a fine-tuning device within the limits prescribed by the thermal characteristics.

It may be that the T_b set point is an integral part of the evolutionary thermoregulatory complex, and, as a result, is to some extent adaptive. (In this case, M_b , C , W , and T_b might be more accurately termed interdependent.) Scholander

et al. (1950c) and most subsequent investigators have concluded that T_b is non-adaptive, but there is now some evidence that mammalian T_b levels may be capable of some adaptive variation independent of M_b , C, and W (McNab, 1970). However, the avian class apparently shows much less variation in T_b than is the case in mammals. This reduces any adaptive effect of T_b , and increases the significance of ecological and climatic impact on M_b and C.

Body Size Effects

The impact of W on thermal relations is considerable. This is largely due to the change in surface : volume ratio with weight. Surface area (A) is theoretically the most satisfactory unit for heat loss calculations, except that it is practically impossible to get an accurate estimate of A. This is especially true in birds, where one would have to decide what surface area must be considered. For example, what relation does A of the exposed parts (legs, head, beak) bear to the feathered surface? Alterations in peripheral circulation, particularly to the extremities, and postural changes complicate definition of the effective surface area. Use of $kW^{2/3}$ as a value of A does nothing to solve these problems; it simply obscures them. Therefore, it is considered that, at present, W is the most undeceptive unit for discussing body-size relations in birds.

The relationship of M_b to W in small birds (<100 grams) has been described empirically by King and Farner (1961) as following an equation equivalent to :

$$M_b \text{ (ccO}_2\text{/g - hr)} = 7.29 W^{-0.341} \quad (9)$$

where W is in grams. Likewise, Lasiewski *et al.* (1967) considered C to be related to W (grams) by the equation:

$$C \text{ (ccO}_2\text{/g - hr } ^\circ\text{C)} = 0.848 W^{-0.508} \quad (10)$$

which is similar to the C equation of Herreid and Kessel (1967). Thus, both M_b and C increase as W decreases. However, M_b increases less rapidly with small size than does C, and the thermoregulatory quotient increases as W increases:

$$\begin{aligned} (M_b/C)_e &= 7.29 W^{-0.341} / 0.848 W^{-0.508} \\ &= 8.59 W^{0.167} \end{aligned} \quad (11)$$

where W is in grams. So, it can be seen that a species can attain a given $(T_b - K)$ either by adaptively changing $(M_b/C)_r$ or by possessing a suitable body size $(M_b/C)_e$. The effect of W on $(T_b - K)$ when $(M_b/C)_r$ is constant is shown in Figure 18.

McNab (1969) suggested that there is a "critical" weight in mammals below which T_b is dependent on W, but above which T_b appears to be independent of W. Departure of $(M_b/C)_r$ from 1.0 can compensate for W changes, and thus alter this "critical" weight. A "critical" weight is also indicated for birds (McNab, 1966a, 1970). So far as can be determined from published accounts and the data presented here, T_b in birds appears to be W-dependent throughout the size range, with the highest T_b values occurring at about 20 grams. Above this size, T_b declines very gradually, and below it, precipitously. Much of the data scatter is probably due to the $(M_b/C)_r$ effect. Apparently the "critical"

weight is also variable. In warblers it occurs at 10-11 grams, in flycatchers at about 15 grams, and at 18-20 grams in sparrows. The significance of these apparent differences is not now obvious, although it may be similar to the case in mammals (McNab, 1970) in which temperate species have lower K values than tropical forms.

Precision of T_b Regulation

The birds studied to date fall into two categories:

(1) those that regulate very well at moderate T_a at all times until W (energy) loss results in weakening and death, and
 (2) those that regulate very well at T_a of 10-30 °C but can go into torpor in times of stress or inactivity (humming-birds, goatsuckers, some swallows and swifts). Thus T_b in birds would superficially appear to be less sensitive to T_a changes than is the case in many mammals. It should be noted, however, that most of the species of birds which one would suspect as being poor thermoregulators are found in the tropics. The physiology of tropical birds is essentially untouched.

Birds employed in the present study are adequate to good thermoregulators. The change in T_b per unit change in T_a ($\Delta T_b / \Delta T_a$) is a measure of the sensitivity of T_b to T_a . Figure 21 shows that there is little change in T_b over T_a from 30° - 10°C. Although there is a greater change in the smaller species of each family or those having a low $(M_b/C)_r$, the poorest thermoregulator is precise when compared with values for some mammals (McNab, 1966b, 1969). Values of $\Delta T_b / \Delta T_a > 0.10$ are found only in those species with both very small

Fig. 20. A plot of the extent to which body temperature is buffered, as a function of the combined ratios $(M_b/C)_r$ and $(M_b/C)_e$. The line is expected from Newton's law of heat loss. See Tables 1 and 2 for data and references.

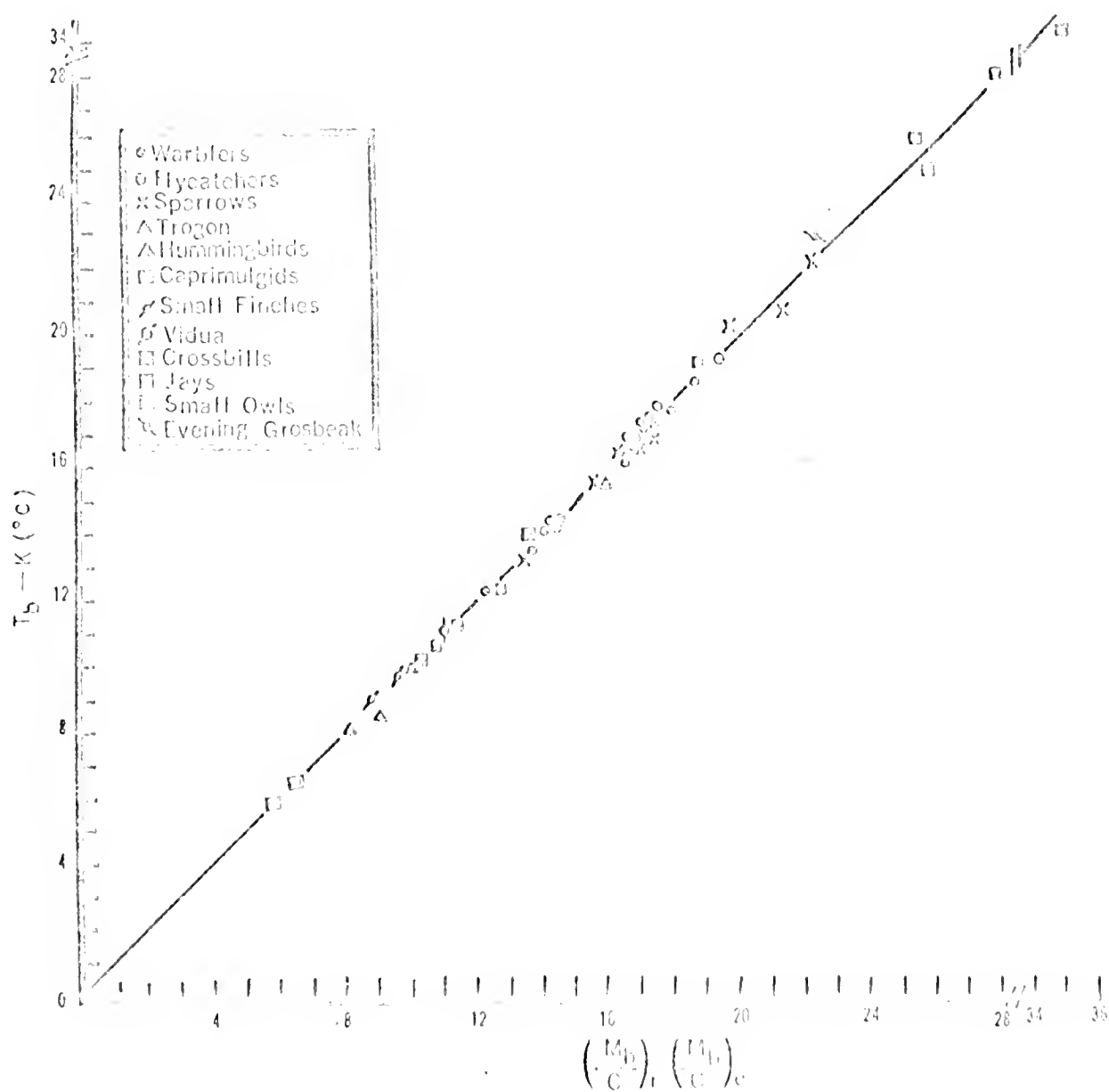
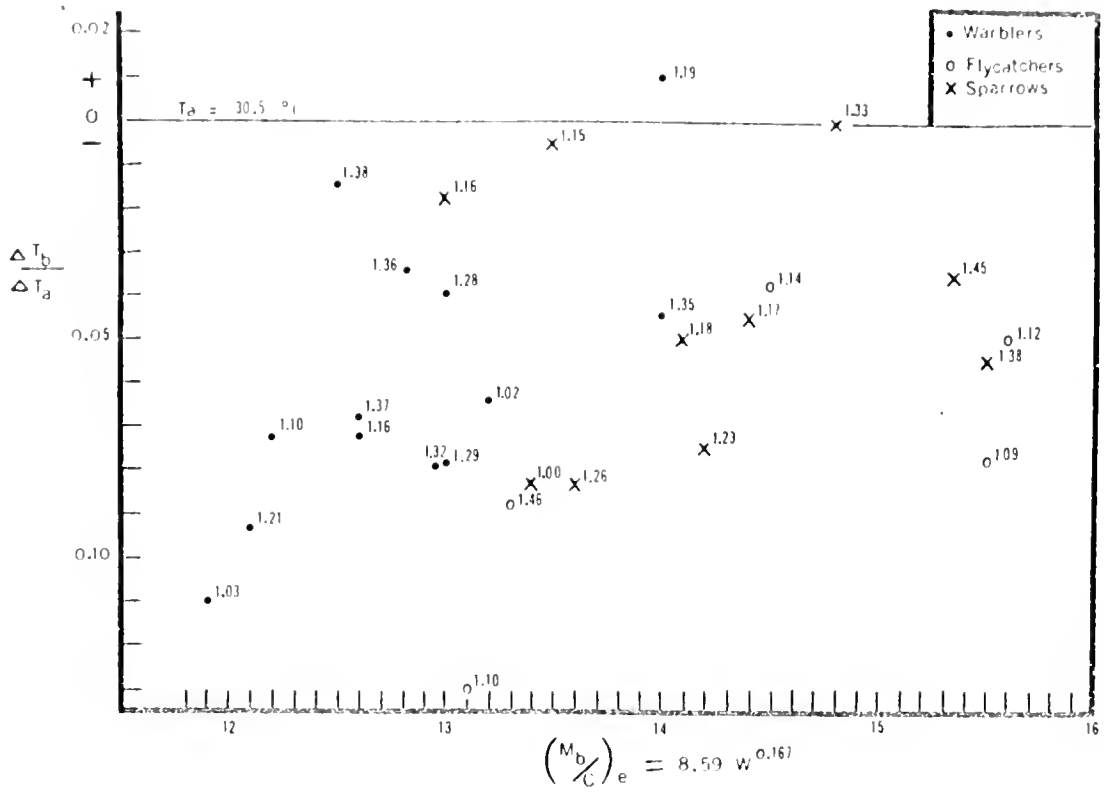


Fig. 21. A plot of the degree of sensitivity of body temperature to changes in ambient temperature ($\Delta T_b / \Delta T_a$) as a function of body size $(M_b/C)_e$ in some small birds.

Fig. 22. The relation of body weight and the ratio $(M_b/C)_r$ to the lower limit of thermoneutrality. Arrows indicate the climatic zone which is the wintering limit for each general food habit type. See the text for further explanation, and Tables 1 and 2 for data and references. Symbols are as in Fig. 20.



body size and low $(M_b/C)_r$, the Parula Warbler and the Acadian Flycatcher.

The amount of energy reserves (fat) is an important factor in the precision of regulation. Weight deviations greater than five per cent from the species mean are positively correlated with T_b deviations greater than 0.5 °C from the species mean. Such an analysis will account for 83 per cent of the variation in warblers, 77 per cent in flycatchers, 61 per cent in *Zonotrichia* sparrows, and 100 per cent in sparrows smaller than 20 grams.

Adults of small species with altricial young probably live near the limits of their energy reserves during the breeding season, particularly during the nestling period. This is an especially acute problem for insectivorous species, if that season happens to have frequent inclement weather. The frequency of thunderstorms during the nestling period of 1969 was abnormally high in eastern North Carolina. Results of several metabolic tests of the small flycatchers (particularly the Acadian) had to be discarded because the birds were in such poor nutritional condition. If Acadians were captured before noon prior to nocturnal testing, sometimes they would weaken and die by the following morning. Even in a species that forages and flycatches, such as the Blackpoll Warbler (*Dendroica striata*), body lipid content may be almost completely exhausted during parts of the breeding season (Yarbrough, 1970a).

Ecological and Distributional Relationships

Some of the ways in which ecology and climate may affect

the behavior of various thermoregulatory parameters have been discussed above. It is my intent in this section to summarize some of the general relationships that exist between the physical model and patterns of avian distribution.

Consideration of all the factors in the heat loss model accurately accounts for non-experimental variation in the data (Fig. 20). The various species spread out along the theoretical line, with very small birds or desert and tropical species nearest the origin, and birds that are larger or adapted to cold T_a farthest from the origin.

A more meaningful representation of this information is given in Figure 22. The lowest thermoneutral T_a for a species is connected with the origin. The data point is placed where this line intersects a line between the weight and $(M_b/C)_r$ characteristics for the species under consideration. These thermoregulatory parameters can then be related to climatic or latitudinal distribution. The climatic zone which is the winter thermal limit for birds having certain food habits is also indicated. The picture could be more precise if we understood the impact of ecological factors other than food habit on the distribution of birds.

Lines A, B, and C are empirical thermo-ecologic boundaries for small birds up to about 100 grams in weight. Movement from one zone to another is possible by changing W or $(M_b/C)_r$. For example, the birds in the tropical-desert

zone are not generally cold-stressed in nature and have become adapted for coping with heat stress and water scarcity. This may involve being very small (small finches and Paradise Widowbird) or having a low thermal index ($T_b - K$), such as that of the Black-throated Trogon and some caprimulgids. The capacity for torpor serves as a buffer to reduce energy outlay in times of food deprivation and occasional cool weather.

Birds wintering in the cold-temperate to subarctic zone must have a high $(M_b/C)_r$ and cannot be smaller than about ten grams. The thermoregulation of northern chickadees (*Parus hudsonicus* and *P. cinctus*) should be examined from this standpoint. Food habit is usually limiting in this zone, since only herbivores and carnivores (including scavengers, such as gulls and ravens) are found here. Steen (1958) has found that some small, cold-climate species can allow T_b to drop as low as 30 °C at night as an energy conservation measure. He also suggests that under natural conditions these birds avoid severe cold stress by means of their roosting habits.

The majority of species used in this study fall into the temperate zone, having K values between 22° and 25° C. It is of interest to note that all the flycatchers studied, except the Acadian, are thermally capable of wintering in the temperate zone. This is an obvious case of avian distribution being limited by food habit (and possibly evolutionary history). The warblers that winter as far north as

the southeastern U. S. fall into zone C (temperate), whereas those that winter from the Caribbean area southward fall into the subtropical zone on the graph. The winter range of the Pauraque does not extend as far north as that of the Poor-will. Yet, on a thermal basis the Pauraque is much better equipped to regulate at low T_a . It would be germane to know if the Pauraque can or does enter torpor as readily as the Poor-will. The lower M_b of the Poor-will may indicate a greater external heat load than is true for the Pauraque.

The three small owls of the southwestern U. S. and Mexico that have been studied are distributed as one would predict from Figure 22. The Saw-whet has thermoregulatory characteristics that coincide with its actual cold-temperate distribution. The Giant Hummingbird has the thermal capability for a subtropical distribution, instead of tropical as is the case with smaller hummingbirds. Its actual distribution extends from the montane tropics southward into Peru and Chile. Range extension of some hummingbirds beyond the thermal limits suggested by their thermoregulatory parameters is probably due to their capacity for torpor.

The present state of knowledge concerning T_b regulation in birds does not allow conclusions to the effect that food habits determine thermoregulatory capacity, as they apparently do in bats (McNab, 1969). Food habit mainly affects the distribution of most birds studied to date. Species with seasonal food problems usually migrate; thus, thermoregulatory

adaptation is unnecessary. There may be correlations of food habit with M_b and C in some species, but other factors such as heat and water stress would complicate any analysis.

In birds, it appears that thermoregulatory parameters are adapted primarily to climate, and are only indirectly or secondarily related to food habit. Therefore, large climatic differences must not be introduced into data that are used to determine the impact of ecology on thermoregulation. Such data have not yet been gathered. Consequently, the need is obvious for extensive studies on tropical birds of all sizes, ecological characteristics, and taxonomic affiliations.

CONCLUSIONS AND SUMMARY

The energetics of T_b regulation in small birds are accurately described by the Newtonian model of heat loss. A thermoregulatory quotient $(M_b/C)_O$ which considers both heat production and the coefficient of heat loss is a more satisfactory indication of thermoregulatory capacity than either parameter alone.

Climatic and ecological adaptations of these parameters are indicated by $(M_b/C)_r$, which compares $(M_b/C)_O$ to the value (1.00) expected from W alone $(M_b/C)_e$. Tropical and desert species generally have low $(M_b/C)_r$, and birds that must tolerate cold climates have high values. Birds living in cool climates may partially compensate, within limits, for low $(M_b/C)_r$ by having an increased body size $(M_b/C)_e$, the capacity for torpor, or both.

M_b may be lower than expected in desert species mainly to reduce the heat load and evaporative water loss. Tropical, non-desert species may also have a lower M_b than expected for other birds in order to reduce the heat load, to conserve energy (if the food supply is unreliable), or simply because they are not faced with the need for a higher rate of heat production. Some cool-climate birds may also have a reduced M_b to conserve energy. This is particularly true if the birds are very small and dependent

on a variable food source (such as insects). In this case, C is also reduced. It is suggested that M_b differences between any two avian groups are actually correlated with ecological and climatic differences in the birds sampled, not taxonomy *per se*.

C is generally high in tropical and desert forms, and low in cold-climate species. However, the effect of environmental stress on M_b may militate against this strategy in some cases. Likewise, M_b cannot be radically altered if the environment precludes compensatory changes in C . M_b and C must evolve as complementary thermal parameters.

The level of T_b is very closely correlated with M_b , C , and W . Non-torpid birds are very precise thermoregulators, as compared to most mammals. A combination of very small body size and a low $(M_b/C)_r$ may reduce the precision of T_b regulation, as may a drastic loss of W during extended food deprivation.

Presently available information indicates that the distribution of avian species outside the tropics and deserts is limited by ecology, particularly food habits. Thermoregulatory parameters are primarily adapted to climate. Thus, in order to determine the extent to which food habit can affect thermoregulation, significant climatic differences must be circumvented. The ecological impact on T_b regulation in birds must remain poorly understood pending investigation of tropical faunas.

APPENDICES

APPENDIX A

Symbols and Expressions Employed in This Paper

Symbol	Description	Units
W	Body weight	Grams
M	Metabolic rate	ccO ₂ /g - hr
M _b	Basal metabolic rate	ccO ₂ /g - hr
M _b %	M _b % expected from W by the King-Farner (1961) equation: $M_b \text{ (ccO}_2\text{/g - hr)} = 7.29 W^{-0.341}$	Per cent
C	Thermal conductance	ccO ₂ /g - hr Δ°C
C%	C% of that expected from W by the equation of Lasiewski <i>et al.</i> (1967): $C \text{ (ccO}_2\text{/g - hr } ^\circ\text{C)} = 0.848 W^{-0.508}$	Per cent
(M _b /C) _o	Observed thermoregulatory quotient	°C
(M _b /C) _e	Thermoregulatory quotient expected from W by the King-Farner and Lasiewski <i>et al.</i> equations (see above): $(M_b/C)_e = 8.59 W^{0.167}$	°C
(M _b /C) _r	Relative thermoregulatory quotient $(M_b/C)_o / (M_b/C)_e$	None
T _b	Body temperature	°C
T _a	Ambient temperature	°C

APPENDIX A

(continued)

Symbol	Description	Units
$\Delta T_b / \Delta T_a$	Change in body temperature per unit change in ambient temperature	None
K	Lower limit of thermoneutral zone	°C
$T_b - K$	Extent of thermal buffering	°C
Q_L	Heat loss	ccO ₂ /g or cal/g
t	Time	Hours
k	Cooling constant	1/hours
A	Surface area	cm ²
c	Specific heat	ccO ₂ /g °C or cal/g °C

APPENDIX B

Scientific and Common Names for Species Discussed in This Study

Species for Which Original Data Are Presented

Sparrows

<i>Spizella passerina</i>	Chipping (W) ¹
<i>Ammodramus savannarum</i>	Grasshopper (W)
<i>Melospiza melodia</i>	Song (W)
<i>M. georgiana</i>	Swamp (W)
<i>Passerculus sandwichensis</i>	Savannah (W)
<i>Pooecetes gramineus</i>	Vesper (W)
<i>Zonotrichia albicollis</i>	White-throated (W)
<i>Z. leucophrys</i>	White-crowned (W)
<i>Z. querula</i>	Harris' (W)
<i>Passerella iliaca</i>	Fox (W)

Flycatchers

<i>Empidonax virescens</i>	Acadian (S)
<i>Contopus virens</i>	Wood Pewee (S)
<i>Sayornis phoebe</i>	Phoebe (W)
<i>Myiarchus crinitus</i>	Crested (S)
<i>Tyrannus tyrannus</i>	E. Kingbird (S)

¹ The symbols indicate the time of year when species were captured and studied: (W) winter, (S) summer, (M) migrant, not in Zugunruhe.

APPENDIX B

(continued)

Wood Warblers

<i>Parula americana</i>	Parula (S)
<i>Vermivora pinus</i>	Blue-winged (M)
<i>V. celata</i>	Orange-crowned (W)
<i>Mniotilta varia</i>	Black-and-white (W)
<i>Dendroica dominica</i>	Yellow-throated (S)
<i>D. palmarum</i>	Palm (W)
<i>D. coronata</i>	Myrtle (W)
<i>D. pinus</i>	Pine (W)
<i>Geothlypis trichas</i>	Yellowthroat (W)
<i>Milvonia citrina</i>	Hooded (S)
<i>Protonotaria citrea</i>	Prothonotary (S)
<i>Seiurus noveboracensis</i>	N. Waterthrush (M)
<i>S. aurocapillus</i>	Ovenbird (M)

Trogon

<i>Trogon rufus</i>	Black-throated
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Species for Which Data Were Obtained from the Literature

<i>Otus trichopsis</i>	Whiskered Owl
<i>Glaucidium gnoma</i>	Pygmy Owl
<i>Micrathene whitneyi</i>	Elf Owl
<i>Aegolius acadicus</i>	Saw-whet Owl
<i>Phalaenoptilus nuttallii</i>	Poor-will
<i>Nyctidromus albicollis</i>	Pauraque
<i>Chordeiles minor</i>	Common Nighthawk
<i>Eurostopodus guttatus</i>	Spotted Nightjar

APPENDIX B

(continued)

<i>Eugenes fulgens</i>	Rivoli's Hummingbird
<i>Lampornis clemenciae</i>	Blue-throated Hummingbird
<i>Patagona gigas</i>	Giant Hummingbird
<i>Vidua paradisaea</i>	Paradise Widowbird
<i>Perisoreus canadensis</i>	Gray Jay
<i>Cyanocitta cristata</i>	N. Blue Jay
<i>Hesperiphona vespertina</i>	Evening Grosbeak
<i>Loxia curvirostra</i>	Red Crossbill
<i>L. leucoptera</i>	White-winged Crossbill
<i>Taeniopygia castanotis</i>	Zebra Finch
<i>Estrilda troglodytes</i>	Black-rumped Waxbill

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BIOGRAPHICAL SKETCH

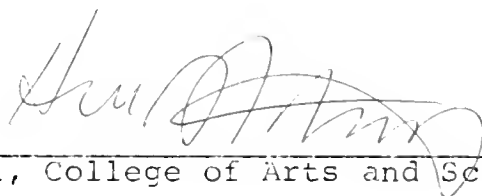
Charles Gerald Yarbrough was born October 13, 1939, at Lumberton, North Carolina. He was graduated from Bladenboro High School (N. C.) in May, 1957. In June, 1961, he received the degree of Bachelor of Science with a major in Biology from Wake Forest University. From 1961 until 1963 he was a teaching assistant and graduate fellow at Wake Forest, where he received the Master of Arts degree in Biology in June, 1963. He attended the University of Michigan as a teaching fellow during the academic year 1963-1964. During the summer of 1964 he did ecological research in the Canadian subarctic on a Chapman research grant from the American Museum of Natural History. He was employed as Instructor in Biology at Campbell College for two years, 1964-65 and 1966-67. During 1965-66 he worked as an Interim Instructor in Zoology at the University of Florida. From September, 1967, until the present time he has pursued his work toward the degree of Doctor of Philosophy while in tenure of a National Science Foundation Traineeship at the University of Florida. In 1968, he worked as an avian ecologist at an Atomic Energy Commission project on Amchitka Island, Alaska.

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This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

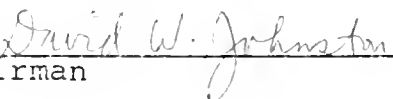
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